

## VIOLA RAFINESQUII, THE ONLY MELANIUM VIOLET NATIVE TO NORTH AMERICA

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While associated at the Biology Department of Vanderbilt University in the spring of 1961, the authors had occasion to study the annual wild pansy, *Viola rafinesquii* Greene, in the vicinity of Nashville, Tennessee, and to determine the chromosome number of local representatives of that species. The information obtained, combined with previously unpublished experiments by the senior author, now makes it possible to corroborate that this plant is an indigenous North American species, a member of the otherwise Old World *Melanium* section of *Viola*.

### SEASONAL DIMORPHISM

The North American field pansy, *Viola rafinesquii*, shows a characteristic seasonal dimorphism that has generally been overlooked: its early spring flowers are chasmogamic and have moderately large, showy petals; as the season moves towards late spring and early summer the same plants bear cleistogamic flowers that have tightly closed sepals, small or no petals, and fewer anthers that empty their pollen directly into the stigma. This inconspicuous cleistogamic stage is frequently overlooked.

Whether or not chasmogamic flowers develop appears to depend upon the season in which the seedlings germinate. Viola Brainerd Baird (1942, p. 204), possibly referring to some of her father's experiments, reported that *Viola rafinesquii* bears closed flowers in great abundance through a long growing season. If the seeds germinate in the fall, the seedlings produce open flowers in the spring followed by closed ones, but if they are germinated in the spring only closed flowers are produced. This is a behavior typical of a vernalization mechanism, possibly triggered by winter chilling.

Under natural conditions *Viola rafinesquii* possesses a

regular alternating pollination system: most of the seeds are produced within the tightly closed late spring and summer flowers by self-pollination, but during the early spring season there is a flush of open, showy flowers, providing possibilities for cross-pollination. In this respect the North American field pansy differs from its ca. 50 Old World relatives among which cleistogamy has not been observed.

The seasonal dimorphism of *Viola rafinesquii* is as striking as that in the classical example of *V. mirabilis* L. of the *Nomimium* section. Both species carry their cleistogamic flowers on erect stems. In contrast, our North American stemless blue violets of the *Plagiostigma* section and the European *V. odorata* L. of the *Uncinatae* have no elongated aerial stems and carry their cleistogamic flowers on decumbent pedicels, tending to bury their seed capsules in the ground.

The changes that occur in the floral development from the chasmogamic to the cleistogamic stage are remarkably coordinated. The petals gradually disappear, the number of anthers is reduced, and the style changes its growth, placing the orifice of the stigma below the remaining anthers. In *Viola mirabilis* the senior author observed that it is the two anthers adjacent to the lower, aborted spur-bearing petal that remain, and only two of the four anther lobes of each function, reducing the number of pollen mother cells to approximately four per lobe. In contrast, in *V. rafinesquii* only one anther remains in the fully cleistogamic flower. This is the upper anther between the aborted two upper petals, and the style performs a corresponding twisting growth that insures the receptance of the pollen in the stigma under these conditions. It is noteworthy that violets of distinct sections have evolved such different solutions to cleistogamic fertilization.

In *Viola rafinesquii* the early spring and summer forms are so different that superficially they could pose as distinct species. Such seasonal difference of form has delayed a recognition of the true nature of the species and has resulted in a highly confused taxonomic history.

## TAXONOMIC HISTORY

The earliest known collection of the North American field pansy is Clayton's *Viola* No. 527, listed as a descriptive polynomial in Gronovius' *Flora Virginica*, 1739-1743. According to Fernald (1939), Gray in 1839 established the identity of the polynomial and annotated the entry as *V. tenella*.

The North American pansy was originally named by Rafinesque in 1808 as *Viola tenella*, a *nomen nudum* (Med. Repos. New York 5: 538, 1808) designating a North American violet. In 1813 Muhlenberg (Cat. 26) also listed *V. tenella*, but he probably obtained the name from Rafinesque; he also used it in the same sense. During 1818 and 1819 Rafinesque travelled in Kentucky and adjacent states (Fitzpatrick, 1911 pp. 24-26), the central region of the American field pansy, and in 1819 he validated *V. tenella* (The American Monthly Magazine and Critical Review 4:191, 1819). By this time, however, Poiret (1810) had long ago used the binomial *V. tenella* for a Syrian relative of *V. kitaibeliana* R. et S.

Frederick Pursh (1814, I:175) listed this North American violet as *Viola bicolor*, a common pre- and post-Linnaean synonym for *V. arvensis* Murr. (1770). Pursh did not claim *V. bicolor* to be a new species. The name was adopted from Hoffman's *Flora Germanica* 2:170 (1807), where it applied to one of the many segregates of *V. arvensis* Murr. Pursh mentions (Preface, p. xiii) that his Compendium was published on the plan of Hoffman's *Flora Germanica*.

Neither did Pursh claim *Viola bicolor* to be an indigenous North American species. On the contrary, he states in I, p. 175, that it "nearly approaches *V. tricolor*. Specimens in the collection of A. B. Lambert, Esq. from Pallas' herbarium are the same with this species". These specimens were North-Asiatic (Preface xvi) and accordingly belonged to the *V. tricolor-arvensis* complex, not to the North American species.

Nuttall (1818, p. 151) provided more information about Pursh's species, which he catalogued as "*V. bicolor* ? Hoffm.

Fl. Germ. 2, p. 170 and Pursh I, p. 175" with the synonym *V. arvensis* Elliott. Nuttall's description fits the vernal form of the North American pansy, and he adds significantly: "Closely related to *V. tricolor*. Apparently native".

In order to understand the use of the epithet *Viola bicolor* one must keep in mind that botanical legislation is a recent procedure and that taxonomic usages were lax in the transition period following Linnaeus' introduction of binomial nomenclature 200 years ago. *Viola arvensis* and *V. bicolor* were considered synonymous and were commonly thought of as being only varieties of *V. tricolor* until the beginning of the present century.

The epithets "tricolor" and "bicolor" were originally used descriptively for the two color "varieties" of the European field pansy, namely *tricolor*, for the ivory-yellow-violet large-petaled form which became the type of the species of that name, and *bicolor*, for the ivory-yellow small-petaled form which eventually became *Viola arvensis*. The friend and frequent correspondent of Linnaeus, Albert Haller, had polynomially described the latter as "*V. bicolor. V. arvensis*, flore candido et luteo", meaning a violet of cultivated fields, having ivory and yellow flowers (Flora Jenensis, 1748, p. 287). Linnaeus himself (Sp. Pl. 936, 1753) used the binomial *Viola tricolor* for the species but listed the trinomial *V. bicolor arvensis* Bauhin as a synonym for *tricolor*. Murray (1770) recognized the ivory-yellow small-petaled form as a species, validating the epithet *V. arvensis* for it instead of *V. bicolor*. Nevertheless, *arvensis* continued to be considered a variety of *V. tricolor* throughout the next 150 years.

The long-established usage of the epithet *Viola bicolor* persisted, however, beyond both Linnaeus and Murray. In old herbaria one often finds the name *V. bicolor* appended to specimens of *V. arvensis* of both pre- and post-Linnaean age. Gilbert's *Flora Lithuanica* (1781), listing *V. bicolor*, continued the practice. Hoffman (1807) in his *Flora Germanica* included a description of *V. bicolor*, having no idea that in later botanical legislation this act would validate the epithet. Pursh (1814) innocently perpetuated this epithet for a North American species.

The name *Viola bicolor* has therefore been a long-persisting source of botanical confusion. In relation to the North American species it must be rejected as a later homonym for the illegitimate *V. bicolor* Hoffman and as a source of confusion.

During the Asa Gray period (Torrey and Gray, 1838, p. 143; Gray, 1858, p. 144) the American field pansy was generally assumed to be an introduced form of the European *Viola tricolor* L. var. *arvensis* (Murr.) D. C. Later on it was suggested (Gray 1875, p. 80; 1889, p. 81; and 1895, p. 204) that the variety seemed like a native plant, but it was still not legitimately named and was referred to as *V. tenella* Muhl.

Greene (1899) was the first to provide a valid, legitimate name for Rafinesque's pansy, sensibly renaming it *Viola rafinesquii*, and this has been its name until fairly recently. Greene was the first to call attention to the fact that the vernal and summer forms of this species are very different, and he also recognized the species as the only North American relative of the Old World pansy group of violets.

Ezra Brainerd (1908 in Gray's *New Manual* p. 587; 1911; 1913 in Britton and Brown II:562-563; and 1921:164) clearly distinguished between *Viola rafinesquii* as a native species, and *V. arvensis* and *V. tricolor* as species introduced to North America from Europe. The illustrations accompanying Brainerd's treatment of the three species in Britton and Brown's *Flora* clearly render the characteristic morphological differences; the *V. rafinesquii* figure closely resembles the Tennessee form of that species, whereas the color plate in the 1921 book is of a distinctly different Kansas form of the species. Gleason (1952) in the third edition of Britton and Brown's *Flora* also correctly distinguishes the three species.

Brainerd's taxonomic descriptions do not refer to the seasonal dimorphism of *Viola rafinesquii*. His writings indicate, however, that he was highly conscious of the biological significance of cleistogamy in many North American violets. He extensively grew his plants for observation and

experimentation. Viola Brainerd Baird (1942), possibly referring to her father's experiments, reported that the time of the germination of the seeds of *V. rafinesquii* determines whether a stage of open flowers will precede the cleistogamous one, as was discussed under seasonal dimorphism.

In contrast to Greene and Brainerd, Fernald (1938, 1951) concluded that *Viola rafinesquii* is not native of North America. He regarded it as an introduced form of *V. kitaibeliana* Roem. et Schult., a weedy species of central to southern Europe and west Asia that until about 40 years ago commonly was considered to be another variety of *V. tricolor*. Fernald was influenced by his keen field observations that *V. rafinesquii* is now a rapidly spreading weedy plant along roadsides in the southern states, east of the Rocky Mountains. This is undoubtedly the case, but weedy nature does not prove that a plant is a foreigner, as Shinnars (1961) has pointed out. Many indigenous species thrive on disturbed soil and utilize the new opportunities provided by the activities of man.

Influenced by A. J. Wilmott of the British Museum, Fernald (1938) named the North American plant *Viola kitaibeliana* var. *rafinesquii*, suggesting that the plant had possibly changed since it arrived in North America more than 200 years ago. Fernald discussed minute ciliation characters as criteria of identity but was silent on the real important differences, such as cleistogamy. He failed to notice that his figure 1 of Plate 526 is of a large-petaled chasmogamic spring form, and figure 2 of a cleistogamic summer form of *rafinesquii*, whereas *V. kitaibeliana* has open flowers and petals that are even smaller than in *V. arvensis*. We agree with Shinnars that plants similar to the Eurasiatic *V. kitaibeliana* have never been recorded from North America. Neither has the American *V. rafinesquii* ever been reported from Eurasia or North Africa.

Although Shinnars (1958) adopted the name *Viola bicolor* Pursh for the American field pansy in his Dallas Flora, the discovery of the existence of the earlier homonym *V.*

*bicolor* Hoffmann has led him subsequently (1961) to resume the use of *V. rafinesquii* Greene. Shinnars has presented convincing circumstantial evidence that the Rafinesque violet is native to North America, a point with which most students of the species will agree.

It is our purpose to present additional evidence in support of the native status of this plant.

#### DISTINCTNESS OF VIOLA RAFINESQUII FROM ITS EUROPEAN RELATIVES

*Viola rafinesquii*, *V. tricolor*, *V. arvensis*, and *V. kitaibeliana* are morphologically closely related and form a species complex. Typically flourishing under disturbed conditions, these species are all weedy in nature, although they also occur in undisturbed habitats.

The characteristic features of the four species of the *Viola tricolor* complex are presented in Table 1. *Viola rafinesquii* is unique among them in being seasonally dimorphic: its early spring flowers are open and have showy petals, but in late spring and early summer the flowers gradually become closed, having no petals or only rudimentary ones. The cleistogamic, inconspicuous but heavily fruiting stage is poorly represented in herbaria.

*Viola rafinesquii* differs also from the other three species of the *V. tricolor* complex by having slender stems, a character to which the earliest epithet, *tenella*, referred. It is further distinguished by roundish, almost entire basal leaves, and by pectinate, palmately divided stipules. The petals of its open flowers are twice as long as the sepals, slightly shorter than the petals of *V. tricolor* but much longer than those of *V. arvensis* and *V. kitaibeliana*.

The petal color of *Viola rafinesquii* is either bluish white or blue, and both color forms may occur in the same populations. Wild *V. tricolor* in contrast has violet-purple or deep yellow petals, and *V. arvensis* and *V. kitaibeliana* both have ivory petals.

*Viola rafinesquii* is a winter annual like *V. arvensis* and *V. kitaibeliana*. The weedy forms of *V. tricolor* are also

Table 1  
Distinctions among the species of the *Viola tricolor* complex

Characters:	<i>V. rafinesquii</i> :	<i>V. tricolor</i> :	<i>V. arvensis</i> :	<i>V. kitaibeliana</i> :
Stem	slender	fairly robust	robust	fairly robust
Life duration*	annual	perennial and annual	annual	annual
Leaf dentation	almost entire	crenate	crenate	crenate
Lower leaves	rounded	ovate to elongate	ovate to elongate	rounded to elongate
Stipules	palmate-pectinate	palmate to pinnate	pinnate	pinnate
Flowers	chasmogamic, becoming cleistogamic	chasmogamic	chasmogamic	chasmogamic
Petal length	9 mm. becoming none	10-12 mm.	5 mm.	2-3 mm.
Petal color	bluish white or deep blue	violet purple or deep yellow	ivory	ivory
Pollination	outcrossing and cleistogamic	cross-pollinating	selfing	selfing
<i>n</i> =	17	13	17	7, 8, 12, 18, and 24 in plants morphologically similar.

\*All annual forms are plants of disturbed soil and weedy in nature.

Perennial forms of *V. tricolor* are plants of dunes and coniferous forests.



annuals, whereas its races from uncultivated habitats, such as coastal dunes and coniferous forests, are perennials.

*Viola kitaibeliana* and *V. arvensis* are both habitual self-pollinators; *V. rafinesquii* alternates between opportunities for cross-pollination and forced self-pollination, whereas *V. tricolor* is structurally prevented from self-pollination. The perennial dune form of *V. tricolor* suffers severely by inbreeding, but the weedy forms of that species are self-compatible and can be inbred similarly to *V. rafinesquii*, *V. arvensis*, and *V. kitaibeliana*.

*Chromosomal and cultivation evidence* — *Viola rafinesquii* has 17 pairs of chromosomes. This number was previously established for plants grown from seeds of the Brainerd stock furnished by Alexander Gershoy (Clausen, 1929, and Gershoy, 1934). The plants of this stock were morphologically identical with the Brainerd color plate (1921) based on plants from Baldwin, Kansas (Baird, 1942, pp. 204-205; p. 214).

Counts of  $n = 17$ ,  $2n = 34$ , were made by Nur in 1961 from morphologically different plants from several localities in the vicinity of Nashville, Tennessee, specifically for the present paper (cf. Channell voucher specimen No. 8878, VDB). The same number has now been reported from Texas by Walter H. Lewis (Shinners, 1961). The counts suggest that *V. rafinesquii* is chromosomally constant through three separate regions.

*Viola arvensis* happens to have the same chromosome number,  $n = 17$  (Clausen, 1921, 1922), as *V. rafinesquii*. *Viola tricolor* has a different number,  $n = 13$ , and in Europe it hybridizes spontaneously with *V. arvensis* despite their differences in chromosome numbers (Clausen, 1921, 1922, 1931); the hybrids have reduced fertility and second generations have reduced vigor. *Viola arvensis* and *V. tricolor* are rare weeds in the eastern and the northwestern United States but natural hybrids between these and *V. rafinesquii* have not been reported.

In contrast with the constancy of the chromosome number in each of the former three species, the number is highly variable in *Viola kitaibeliana*, where plants of similar mor-

phology have  $n = 7, 8, 12, 18,$  and  $24$  chromosomes (Clausen, 1927, 1929, 1931).

In cultures, *Viola rafinesquii* is more specialized in its requirements than the other three species. The Kansas strain received from Gershoy in 1926 was grown for five successive years in the experiment garden of the Genetics Department of the Royal Agricultural College at Lyngby, near Copenhagen, Denmark, and during 1932-1934 in the experiment garden of the Carnegie Institution of Washington at Stanford, California. *Viola rafinesquii* was weak and grew poorly out-of-doors in Denmark and California, although it is an aggressive weed in the eastern United States. In both environments the plants exhibited distinctly dimorphic flowers.

By contrast, *Viola tricolor*, *V. arvensis*, and *V. kitaibeliana* were all highly vigorous, both in Denmark and in California, indicating adaptabilities outside their natural ranges not shared by *V. rafinesquii*. The differences in range of tolerance may be taken as ecological evidence that *V. rafinesquii* is distinct from the other three.

*Evidence from crossing attempts* — In 1933 a series of crossing experiments was performed at Stanford in order to ascertain the degree of genetic relationship between the Kansas line of *Viola rafinesquii* and its three supposed European relatives. Chasmogamic flowers of *V. rafinesquii* were used for the crossings. "Key lines" of the three European species were used, which in many previous experiments had proved to be good "combiners" (Clausen, 1931). All lines, except one, were crossed reciprocally, with several flowers of each line being used for the crossings. The combinations were as follows:

1766-1 <i>V. rafinesquii</i> $n = 17$	{	<ul style="list-style-type: none"> <li>× Line 504, <i>V. tricolor</i>, Emmerlev, South Jutland, <math>n = 13</math></li> <li>× 1765, "<i>V. kitaibeliana nana</i>" <i>V. nana</i> (D.C.) Corbiere Channel Islands, <math>n = 24</math></li> <li>× Line 142, <i>V. arvensis</i>, Tysinge moor, Sjaelland, <math>n = 17</math></li> </ul>
		(all reciprocally)

Line 52, *V. arvensis* × 1766-1, *V. rafinesquii*,  $n = 17$  (not reciprocally)  
Allindelille, Sjaelland,  
 $n = 17$

Only empty seeds were obtained as a result of crosses involving *V. rafinesquii*. In all other combinations the three European species produced abundant seeds, good  $F_1$  plants, and usually fair-sized  $F_2$  populations (Clausen, 1931). The *Viola rafinesquii* parent also produced many good seeds when selfed.

The failure of *Viola rafinesquii* to cross with any of these species is therefore of considerable significance. Unquestionably the four species are morphologically related, but at least the Kansas form of *V. rafinesquii* is apparently separated from the other species by strong genetic barriers.

*Geographic and edaphic distribution* — The prevailing taxonomic confusion makes it presently difficult to determine the range of *Viola rafinesquii* with certainty. It is a delicate plant that grows in patches and colonies, often exhibiting one color form alone (pale bluish white or blue) or both color forms together.

The species appears to range from New York into Michigan and into Indiana, and westward into Nebraska and Colorado. Southward it ranges through New Jersey into Florida and westward into Texas and Oklahoma. This is a large area for a single species and much larger than that of most of the species outside of the *V. tricolor* complex. The regional climate of the eastern United States contrasts sharply with the climate of western Europe and western North America, but it is sufficiently diversified to admit more than one climatic ecotype.

Edaphically, *Viola rafinesquii* is a species of fields and open woods, of roadsides and waste places. It occurs on sandy soils, sandy clay, on calcareous shale, and on limestone. Its ability to range from sand to limestone indicates an unusual range in edaphic tolerance. In Europe, *V. tricolor* is primarily limited to acid, sandy soils and *V. arvensis* to calcareous soils of high ph values, whereas hybrid colonies occur on soils of medium ph (Clausen, 1922). It is there-

fore to be expected that edaphically distinct ecological races may exist superimposed upon series of climatic races in this species.

*Discussion* — It is a puzzling situation that a single *Viola* species of the section *Melanium* is native to eastern North America, whereas the other 20 to 50 species of the section, depending upon the species concept (Becker, 1910), occur on the other side of the Atlantic Ocean and are primarily European. *Viola rafinesquii* occurs over an area approximately the size of that occupied by the major bulk of the chromosomally and morphologically highly variable European pansy species, yet it is relatively uniform. It also is the only species of the section that bears cleistogamic flowers.

The *Viola rafinesquii* chromosome number,  $n = 17$ , appears to be derived. It is a rare number in the genus but is repeated in Europe in the widespread *V. arvensis* and in three rare endemics, namely, *V. rothomagensis* Desf., endemic to limestone areas of northern France, and in *V. eugeniae* Parl. and *V. pseudogracilis* Strobl, both montane, narrow endemics of the central and southern Apennines of Italy (Schmidt, 1961).

The inconspicuous *Viola kitaibeliana* seems to be the chromosomally most primitive pansy species. It possesses a rather wide range of chromosome numbers but is morphologically uniform. Although having uniformly small ivory petals, it apparently possesses genes for most petal colors and petal sizes, but genetic studies have shown that these are suppressed by inhibitors (Clausen, 1931).

Certain evolutionary generalities are contradicted by the fact that the partially sympatric European species of the *Melanium* section have retained compatibility and the geographically highly isolated *Viola rafinesquii* acquired genetic isolation from its morphologically close relatives on the other side of the Atlantic Ocean.

*Viola rafinesquii* gives the appearance of a uniform, rather primitive species. It is not possible to determine whether in the long past it migrated from Europe and in that process diverged genetically from the other members of the section

or whether the progenitors of the section left it behind in a migration eastward. In any case, the Old World species of Section *Melanium* have obviously experienced a far more lively evolutionary flourish than the single survivor in the New World, which has not been able to colonize the region west of the Rocky Mountains.

#### SUMMARY

*Viola rafinesquii* is a native eastern North American species of the otherwise Old World section *Melanium*, the highly distinct pansy section of the genus. It differs from all other species of that section by having seasonally dimorphic flowers: its early spring flowers are open and have large and showy petals, whereas in late spring to early summer the flowers become cleistogamic and closed, having rudimentary to no petals. In achieving cleistogamy *V. rafinesquii* follows a pattern in reduction of anthers that differs from the classical example of *V. mirabilis*.

*Viola rafinesquii* has had a turbulent nomenclatorial history and at various times has been associated with each of three European members of *V. tricolor* complex. It is, however, morphologically distinct from all of them by a combination of many characters.

*Viola rafinesquii* occurs sporadically throughout the southeastern and central parts of the United States east of the Rocky Mountains. It extends over at least 10 latitudes and occupies habitats that range from sand to limestone. Within each climatic zone it takes advantage of man's activities, has become weedy, and is in the process of extending its range (Shinners, 1961). Beyond its natural climatic range it was unsuccessful in transplantation to Denmark and California. In contrast, its European relatives are more adaptable, growing successfully in the latter two areas.

*Viola rafinesquii* has  $n = 17$  pairs of chromosomes, the same number as in *V. arvensis* and in the rare endemics *V. rothomagensis*, *V. eugeniae* and *V. pseudogracilis*.

Attempts to cross *Viola rafinesquii* with good combiners belonging to *V. tricolor*, *V. arvensis*, and *V. kitaibeliana*

were unsuccessful, although the three latter species easily cross with each other.

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